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The shape of wind-receptor hairs of cricket and cockroach

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Abstract We examined the exact shapes of the thread-like wind-receptor hairs in the cricket and cockroach. The diameters of hairs at various distances from the hair tip as measured by scanning electron microscopy revealed unexpected hair shapes. We had expected, a priori, that the shape of the hair would be a slender linearly tapered cone, but the measurements revealed hairs in the form of extremely elongated paraboloids. The diameter of the wind-receptor hairs varies with the square root of the distance from the hair tip, i.e., the diameter rapidly increases with the distance from the tip and is asymptotic to the base diameter.

Both the cricket, *Gryllus bimaculatus*, and the cockroach, *Periplaneta americana*, showed the same hair shape. In both insects, the formation of the wind-receptor hair during metamorphosis seems to be controlled by a common cytological program. The shape of the hair constrains the mobility of the wind-receptor hair, because both the drag force caused by moving air and the moment of inertia of motion dynamics are functions of shaft diameter. The shape of the hair is a biological trait which affects the sensory information transmitted to the central nervous system.

Key words Cercal filiform hair · Cricket · Cockroach · Mechanical properties · Wind reception

Abbreviations SEM scanning electron microscopy

Introduction

Crickets, cockroaches and other orthopteran or blattaran insects carry a number of air-motion-sensitive hairs on their cerci. The ability of crickets and cockroaches to sense air motion is important in releasing their predator avoidance (Camhi et al. 1978; Camhi 1980; Gnatzy and Hußlein 1986; Gnatzy and Hustert 1989; Tauber and Camhi 1995). The wind-receptor hairs are, as their name indicates, the principal receptors of viscous force when in contact with moving air (Tautz 1979), and consequently deflect. When the hairs are deflected, they transmit information of the motion of ambient air to a sensory cell under the cuticular wall. The wind-receptor hair is thus regarded as a mechanical interface which converts the velocity of air into the deflection of hair.

The wind-receptor hairs on the cercus of adult crickets have a wide variety of sizes that range from 30 µm to 1500 µm in length and from 1 µm to 9 µm in diameter, and the cercal sensory afferents of the different sized hairs show a frequency-range fractionation (Shimosawa and Kanou 1984a). Shimosawa and Kanou (1984b) explained the range fractionation in the sensory afferents by the difference of mechanical properties due to the size differences. Simply, the mass of the largest hair may be several thousand times that of the smallest, while at the same time, the turning torque due to drag force on the largest hair shaft may be several hundred times greater than of the smallest. They also found that the stiffness of the spring which supports the hair at the base corresponds with the increased hair mass. In the companion paper (Kumagai et al. 1998), the dynamic mobilities of the cercal wind-receptor hairs of different lengths are systematically measured by laser-Doppler velocimetry. The intrinsic mechanical parameters of the wind receptor hair such as the moment of inertia, the stiffness of the hair-supporting spring and the frictional resistance within the hair base, have been found to be length dependent (see Shimosawa et al. 1998). The size is important in serving the function of the wind-receptor hair.

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In addition to size, the shape of hair, i.e., relationship between diameter and distance from hair base, is also important. The diameter of a hair shaft is the main attribute which determines the amount of drag force generated by moving air. The turning torque working on a single hair is an integrated sum of an infinitesimally small torque which is itself the product of the drag force and the arm length from the hair base. The moment of inertia of a hair shaft is also the integrated sum of the second-order moment of mass distribution along the distance from the hair base.

In their model calculation of drag force and hair motion, Shimozawa and Kanou (1984b) assumed, a priori, that the shape of hair is a linearly tapered slender cone, while Humphrey et al. (1993) approximated the filiform hairs of spider and cricket to be a straight cylinder. The linearly tapered cone and the straight cylinder are quite different in shape (Fig. 1). For example, the moment of inertia around the hair base is ten times larger in the straight cylinder than in the linearly tapered cone, if the length and base diameter are the same (see Appendix A). If we try to "adjust" the base diameter of a straight cylinder hair so as to give the same amount of the moment of inertia as that of the linear-cone-shaped hair, the "effective" diameter of the straight cylinder hair would have to be set to $1/\sqrt{10}$. The distribution of drag force, and in turn the amount of hair-turning torque differs depending on hair shape. The shape of the wind-receptor hair therefore seems to be a biological trait which determine the content of sensory information transmitted to the central nervous system.

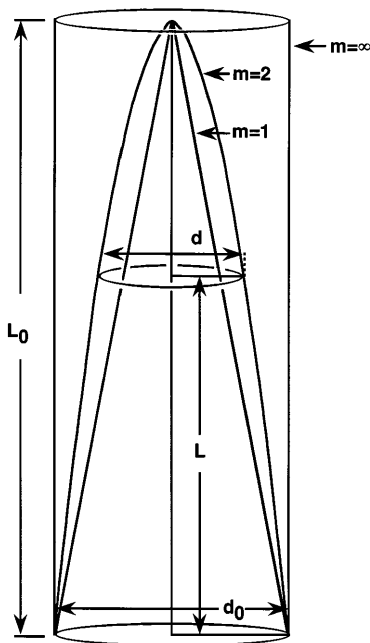


Fig. 1 Schematic drawing of hair shape. Straight cylinder ($m = \infty$), square-root cone ($m = 2$), and linearly tapered cone ($m = 1$) are drawn. Shapes are expressed by shape index m , with which diameter d is given as a power function of height L , $d = d_0(1 - L/L_0)^{1/m}$

The shape of a wind-receptor hair is not necessarily a smoothly tapered cone. Trichobothria, wind-receptor hairs in spiders, have a peculiar shape (Barth et al. 1993). The shaft of a trichobothrium has a feather-like sculptured surface and is curved at its tip. The fine feathery surface arrests the motion of air and increases the effective diameter for drag force generation on the shaft (Barth et al. 1993). There are club-shaped hairs, whose diameter is broader at the tip and narrower at the base, on the cerci of orthopteran and blatteran insects. These are homologous with the wind-receptive filiform hairs on the same cerci and specialized for gravity reception (Walthall and Hartman 1981). The reduction of hair length while keeping the hair mass unchanged causes a selective loss of sensitivity to wind (Shimozawa et al. 1998).

We attempted to analyze the motion dynamics of the wind-receptor hair, based on the systematic measurement of mobility of the hairs (Kumagai et al. 1998) and have revealed a structural scaling in the mechanical design of the hairs (Shimozawa et al. 1998).

For a correct analysis, the accurate estimation of drag force and turning torque was necessary. Here, we examined a geometrical configuration of the cercal wind-receptor hairs of cricket and cockroach by scanning electron microscopy (SEM). Contrary to our initial assumption, we found the shape to be a square-root cone.

Materials and methods

The specimens were males and females of the field black cricket, *Gryllus bimaculatus*, within a week of the imaginal molt, and the adult cockroach, *Periplaneta americana*. Insects with externally intact cerci were selected. The tail portion with the cerci was dissected from the abdomen of the insect. The samples of cerci were washed in acetone, and fixed in ice-chilled 1% osmium (TAAB) solution of cacodylate buffer (pH 7.5) for 1 h. They were washed by the cacodylate buffer solution six times at 10-min intervals. They were soaked in an ice-chilled 1% tannic acid (Nakalai Tesque) solution of cacodylate buffer for 2 h and rinsed with the buffer for 30 min. Specimens were dehydrated in a graded acetone series, and dried by the carbon dioxide critical point drying method. These samples were mounted on a copper sample table (13 mm diameter) by silver paint (Threebond 3350C). After it had been a sputter coated with Pt-Pd, each specimen was observed by a scanning electron microscope (HITACHI S-2400). Among the hairs protruding radially from the cercal axis, hairs which oriented perpendicularly to the microscope axis were selected for the measurement. The diameters of hair shaft were measured at several distances from the hair base (Fig. 1).

Results

The shaft diameters relative to the base size were plotted against the distance from the hair tip relative to the hair length, in a log-log diagram (Fig. 2). The plotted points accumulated through all the measured hairs indicated a linear regression, which implies a power function between the two variables in abscissa and ordinate. If the regression slope is expressed as $1/m$, the relationship

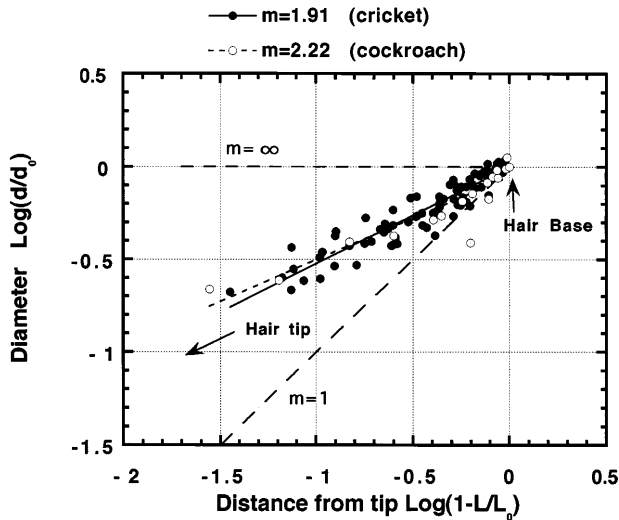


Fig. 2 Relationship between diameter of hair shaft and distance from hair tip. *Filled dots and solid line*: crickets cercal filiform hairs (117 data points). *Open circles and dashed line*: cercal filiform hairs of cockroach (22 data points). *Lines with $m = \infty$ and $m = 1$* indicate the cases of straight cylinder and linearly-tapered cone shape

between diameter d and distance from the base L will be described as follows:

$$d = d_0 \times \left(1 - \frac{L}{L_0}\right)^{\frac{1}{m}}, \text{ or } m = \frac{\log(1 - L/L_0)}{\log(d/d_0)}, \quad (1)$$

where L_0 is the whole length of hair and d_0 is the base diameter.

Parameter m characterizes the shape of the wind-receptor hair, and is hereafter referred to as the shape index. The shape index is given by a function of diameter and height relative to d_0 and L_0 , respectively, whose absolute values characterize the size of hair. The shape index is a size-independent parameter. The value of the index $m = \infty$ represents the shape of a straight cylinder, and $m = 1$ represents the shape of a linearly tapered cone (Fig. 1).

The regression slope $1/m$ for the accumulated data measured from 16 cercal filiform hairs of the cricket whose length ranged between 280 μm and 1200 μm was 0.52 (Fig. 2, solid line). Converted into m , the value of 1.91 was obtained. The cercal filiform hairs of the cockroach also showed similar values of the shape index, although the number of samples examined was small (Fig. 2, open circles and dashed line). The shape of the filiform hairs of the cricket and cockroach can thus be regarded as the elongated paraboloid drawn in Fig. 1 with an exaggerated scaling for diameter.

From the measurements taken at several points of a single hair, we determined the shape indexes of single hair by the same regression method. The mean and standard deviation values of the shape indexes of all cricket filiform hairs measured are 1.91 ± 0.30 ($n = 16$). The shape index appears to be length independent (regression slope = -0.09 in Fig. 3). Thus, all cercal filiform hairs have the same shape index of a square root cone, regardless of length.

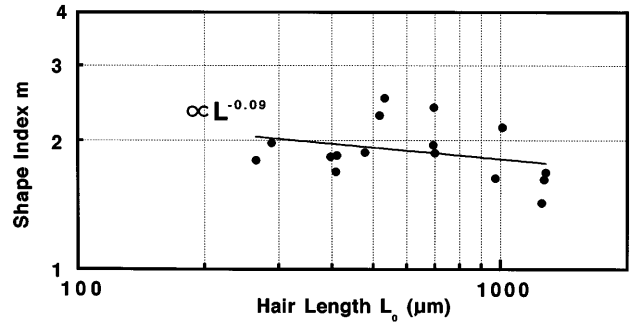


Fig. 3 Length independency of shape index m in cricket wind-receptor hairs

Discussion

As the name filiform or thread-like hair indicates, the cercal wind-receptor hairs of cricket and cockroach are so thin that no further attention to their exact shape has been paid. The present measurement of their geometrical configuration have revealed that the hairs are very slender paraboloids or square-root cones.

In the previous report on the motion dynamics, Shimozawa and Kanou (1984b) assumed, a priori, the shape of linearly tapered cone for the geometrical calculation of the moment of inertia of the hair shaft, and for the drag force estimation. The moment of inertia of the square-root cone is 2.5 times larger than that of the linear cone, if the length and base diameter are the same (Fig. 4 and Appendix A). Our previous calculation of hair motion therefore used an incorrect, under-estimated

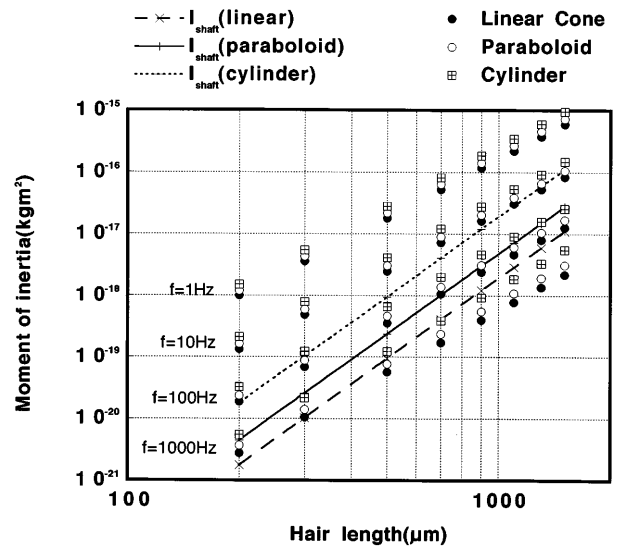


Fig. 4 Effects of hair shape on the moment of inertia of the hair shaft and that due to the added air mass. *Lines*: moment of inertia of hair shaft of different shapes. *Symbols*: moment of inertia due to the added air mass at different frequencies (f). Base diameter varies with hair length by relationship $d_0 = 8.34 \times 10^{-4} \cdot L_0^{0.67}$. Hair shape is important for long hairs and at high frequencies, because the inertial effect of hair shaft becomes larger than that of the added mass

value of the moment of inertia. According to the previous measurement of size of the cricket filiform hair (Shimozawa and Kanou 1984a) base diameter r_0 varies with length L_0 under the allometric relationship of $r_0 \propto L_0^{0.67}$. As the moment of inertia of cone-shaped hairs is proportional to $r_0^2 L_0^3$ (see Appendix A), the amount of moment inertia of a hair shaft should vary as a function of $L_0^{4.34}$. In the companion paper (Shimozawa et al. 1998), the moment of inertia of the wind-receptor hairs of different lengths were estimated by an inverse calculation of motion dynamics by using the systematic data of hair mobility measured for a wide frequency range (Kumagai et al. 1998). The moment of inertia estimated in the companion paper showed the size dependency of 4.32 power of hair length and agrees nicely with the above geometrical estimation of 4.34 power of hair length. According to the electron microscopic study by Gnatzy (1978), the cercal filiform hair of cricket is essentially a thick-wall tube of exoskeletal cuticle. The diameter of the hollow is about one-third of the outer diameter of hair shaft. The moment of inertia of hair shaft may therefore be 10% smaller than that of calculation shown in Appendix A, if the hollow cavity is empty and air filled. It is unlikely that the cavity is completely empty and air filled, because the cavity is sub-cuticular space which is originally occupied by the outgrowth of the trichogen cell and filled with interstitial fluid after the trichogen cell has withdrawn the outgrowth.

In addition to the solid mass of the hair shaft, an air mass which stagnates on and moves with the hair exerts an inertial effect on hair motion (Stokes 1851; Humphrey et al. 1993). The equivalent amount of stagnating air mass varies with frequency of motion. The moment of inertia due to this added air mass is very large compared with that of hair shaft in low frequencies and short hairs (Fig. 4, see Appendix B and Shimozawa et al. 1998 for details of theory and calculation). The moment of inertia due to the added air mass varies with about the 3.1 power of hair length (Fig. 4, symbols), whereas that of the hair shaft varies with about the 4.3 power (Fig. 4, lines). The moment of inertia of the hair shaft is therefore unimportant for the motion of hair at lower frequencies. In addition to the relative unimportance of moment of inertia of hair shaft compared to that of added air mass, in low frequencies the inertial term becomes smaller compared to the viscous drag and spring stiffness terms in the momentum to torque balance equation (Humphrey et al. 1993). Therefore, the shape of the hair as the determinant of moment of inertia of the hair shaft is unimportant in low frequency.

The moment of inertia of the hair shaft, however, becomes dominant in long hairs and at high frequencies (Fig. 4). A fluid dynamic model of hair motion (Shimozawa et al. 1998) shows the effect of this large moment of inertia of a cylinder-shaped hair as the steep reduction of deflection amplitude at higher frequencies (Fig. 5A, triangles).

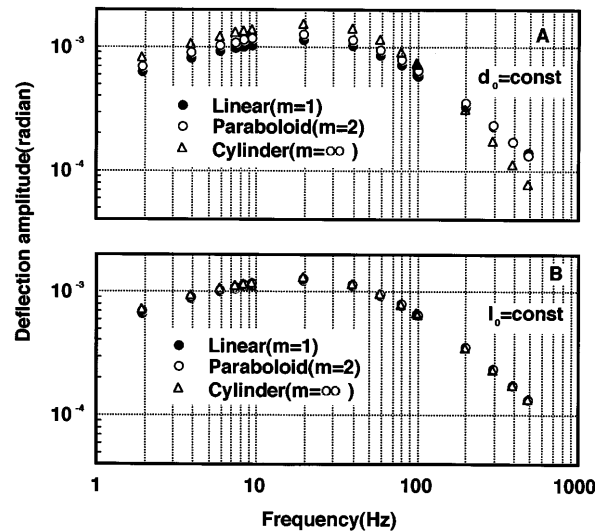


Fig. 5 Effect of hair shape on the dynamic response of a 1000- μm hair. **A** Comparison of deflection amplitude between hairs of different shapes (symbols) with the same base diameter. **B** Comparison of deflection amplitude between hairs of different shapes with same moment of inertia by adjustment of base diameter

Contrary to the ineffectiveness of the moment of inertia of the solid mass of the hair shaft, Fig. 5A shows a shape-dependent difference in deflection amplitude at low frequencies. This difference arises from the fact that the in-phase drag force, as well as the $\pi/2$ -phase-advanced inertial force, is weakly dependent on shaft diameter (see Appendix B and Shimozawa et al. 1998). The deflection of a 1000- μm paraboloid hair is 20% smaller than that of cylindrical hair when their base diameters are the same. In contrast to the shape dependency of deflection amplitude, hairs with different shape deflect in a similar amount, if their base diameter are adjusted so as to have the same amount of the moment of inertia (Fig. 5B). This is because that the adjustment of base diameter from a linearly tapered cone to paraboloid or cylinder shape causes a reduction of shaft diameter over about two-third of the basal portion and an increase in diameter over one-third of the tip portion. The total turning torque does not change because the drag force acting at the tip portion has larger effect on the hair-turning torque than that at the basal portion.

Although the effect of hair shape on the motion of the hair is small except for high frequencies in long hairs, accurate measurement of hair shape was necessary to test the validity of our mechanical model of hair motion. The moment of inertia of the hair shaft geometrically estimated from the shape showed a nice fit with that estimated from the motion of the hair (see Shimozawa et al. 1998).

The geometrical configuration of the wind-receptor hair is formed totally under the cytological program of the trichogen cell (Lawrence 1966; Schmidt and Gnatzy 1971; Gnatzy 1978). It is unlikely that the square-root cone shape is a result of some mechanical forging during

morphogenesis, because no external force, to which mechanical deformation of stress relaxation would occur to untanned hair structure, can be exerted. The formation process of filiform or bristle hair sensillae during development consists of two phases (Lawrence 1966). In the first phase, a mass of cytoplasm filled with microtubules extends from the trichogen cell. The second phase involves the inflation of the cytoplasm of the trichogen cell in the outgrowth of the hair. In this phase, the hair mainly elongates and thickens a little, and the shape is finally consolidated.

Although mechanical forging during morphogenesis is unlikely, the cytological program of cuticular secretion for the square-root cone is likely to be a result of evolutionary optimization having certain biological advantages or mechanical merits. At present, however, we cannot find any simple physics to describe optimization which explains the square-root cone in terms of any possible biological advantages or requirements. For example, the minimization or maximization of the moment of inertia with the same amount of cuticular material would result, respectively, in either $m = 0$ or $m = \infty$; neither is the case. Minimization of the hair material also results in the same meaningless values of m . It is also unlikely that the shape is optimized for mechanical strength of the hair shaft against the drag force of wind. The bending of a hair shaft would be less than 10^{-4} radians for a 1 mm s^{-1} wind. This estimation of bending is based on the deflection of a hair whose base becomes immobile because of the drying up of the inner wet tissue (Kumagai et al. 1998). The hairs would be bent only by 0.1 radians or 5° even by very strong wind of 1 m s^{-1} . In contrast to this small angle of wind-caused bending, the hairs are occasionally pushed down completely by contact with a solid object such as the hind leg of the animal during cleaning behavior. If the internal elastic stress were to exceed the tensile strength of the cuticle, a strong bend of this kind might cause a hair shaft to break.

The increased mechanical strength of the hair shaft against the effects of extreme bending by a solid object thus seems to be reasonable as a biological requirement. To prevent a break, the internal elastic stress of the hair structure due to the strong bend would have to be dispersed uniformly by elastic deformation. The determination of the absolute strength of the elastic shaft against an axial bend requires complex physics on shear stress distribution within the cross section of the shaft (Ohashi 1976). In addition to the complex physics, no exact values of the elastic modulus and tensile strength of the hair cuticle are known; furthermore, the inner structure of hair is not uniform. A single hair shaft is a fascicle of fibrous structures and is fragmented if rolled between two slide glasses with slight compression (T. Kumagai, unpublished observations). We had to give up the attempt to determine the absolute strength of the hair shaft.

We have never seen a broken shaft of a wind-receptor hair in SEM observations of cercal surfaces, although we have seen sockets without hairs. This fact indicates that

the hair shafts have a sufficient safety margin of mechanical strength to resist bending even to the pushing by a solid object. Even though the strength is satisfied, excess strength is not only redundant but also results in a load on the biological economy. The cross-sectional area of a hair shaft can be reduced along the shaft from the base to the hair tip, because the amount of elastic stress to which a portion of hair shaft must be tolerant is the maximum bending torque, i.e., the product of arm length and force applied. The cross-sectional area of the hair shaft can thus be proportional to the distance from the hair tip, while maintaining the same safety margin of mechanical strength as other portions of the hair. This explanation is not of an ultimate biological requirement or constraint upon the shape but of the reduction of an excess safety margin for biological economy.

Although the complicated forms of socket and inner structure of the hair base have been studied (Gnatzy 1976; Gaffal and Theiß 1978; Gnatzy and Tautz 1980), there is no understanding of the cellular mechanism of formation of the complex cuticular structure of hair sensilla. Our present measurements have clarified that wind-receptor hairs in both the cricket, *G. bimaculatus* and the cockroach, *P. americana* are square-root cones, although we have not yet found a simple explanation or interpretation for the shape.

Appendix A

Geometrical calculation of the moment of inertia and the mass of cone-shaped hairs with shape index m

The moment of inertia of a filiform hair for the angular motion around its base is given by the integrated sum of the second-order moment of mass distribution along the length of the rotational arm;

$$I = \int_0^{L_0} y^2 dM, \quad (2)$$

where $dM = \rho\pi r^2 \cdot dy$ is the mass of the infinitesimally thin disk of hair shaft cross-sectioned at height y from the base, L_0 is the full length of hair, ρ is the density of hair shaft cuticle, and r is the radius of the disk. The radius varies with shape index as a power function of height, $r = r_0(1 - y/L_0)^{1/m}$, where r_0 is the base radius, and $m = \infty, 2, 1$ correspond, respectively, to the straight cylinder, the square-root cone, and the linear cone. After replacing variables $(1 - y/L_0)^{1/m} = r/r_0$ with z , therefore $y = L_0(1 - z^m)$, and $dy = -L_0 m \cdot z^{m-1} dz$, the finite integration becomes,

$$\rho\pi r_0^2 \cdot L_0^3 m \int_0^1 (z^{3m+1} - 2z^{2m+1} + z^{m+1}) dz. \quad (3)$$

We obtain the final form of moment of inertia as:

$$I = \frac{m^3}{(m+1)(m+2)(3m+2)} \rho\pi r_0^2 \cdot L_0^3. \quad (4)$$

Therefore,

$$I_{m=\infty} : I_{m=2} : I_{m=1} = 1 : \frac{1}{4} : \frac{1}{10}, \quad (5)$$

if r_0 and L_0 are the same. The mass of the hair can be calculated through a similar treatment:

$$M = \int_0^{L_0} dM = \rho \pi r_0^2 \cdot L_0 \cdot \frac{m}{m+2}.$$

Appendix B

The moment of inertia due to the air mass stagnating around hair shaft is estimated as $I_{am} = C/2\pi f$, where C represents the conversion reactance from velocity to $\pi/2$ phase-advanced torque. Reactance C is given by the integrated sum of the second-order moment of the imaginary part of the mechanical impedance of an oscillating cylinder along hair length,

$$C = \int_0^{L_0} y^2 \cdot \frac{\pi^2 \mu}{g^2 + (\pi/4)^2} dy, \quad (6)$$

where $g = \ln(s) + \gamma$, $s = (a/2)\sqrt{2\pi f/\nu}$, a is cylinder radius, f is the frequency of motion, μ is the viscosity of air, ν is the kinematic viscosity of air, γ is Euler's constant ($= 0.577$), and L_0 is the hair length. A similar integration for the real part of the mechanical impedance gives the conversion resistance from velocity to in-phase torque,

$$D = \int_0^{L_0} y^2 \cdot \frac{-4\pi\mu g}{g^2 + (\pi/4)^2} dy. \quad (7)$$

For details, see Shimozawa et al. 1998.

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